

## Seasonal Migration Patterns and Site Fidelity of Adult Paddlefish in Lake Francis Case, Missouri River

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**Abstract.**—We used ultrasonic telemetry to determine the distribution, seasonal migration patterns, and site fidelity of adult paddlefish *Polyodon spathula* in a main-stem Missouri River impoundment. Thirty-two adult paddlefish collected from two different spring congregation areas in Lake Francis Case, South Dakota, were surgically implanted with ultrasonic tags and relocated monthly from March to November 1994–1996. Paddlefish tagged in the Big Bend tailwaters were captured in this area and in another possible spring congregation (the White River) during pre-spawning and spawning periods, whereas paddlefish tagged in the White River were never located in the Big Bend tailwaters or in areas above the White River. Male and female paddlefish used reservoir habitats similarly except during the pre-spawning period, when male paddlefish used the White River more than would be expected by chance and all females implanted at the White River site remained below the White River. In both the post-spawning and winter periods, all paddlefish moved downstream and congregated in the lower reservoir reaches. Up to 62% of males and 36% of females returned to their original capture site during the presumed spawning period at least 1 of the 2 years after tagging. Thirty-one percent of males at large for 2 years returned to their initial spring capture location each of the following years, but only 9% of females returned. Our results indicate that some paddlefish exhibited site fidelity to the areas where they were captured (i.e., the White River) and presumably attempted to spawn, although winter distribution was similar among all tagged paddlefish. Restoration and stocking efforts may need to focus on habitat management at the locations where paddlefish may spawn, given adequate substrate.

Paddlefish *Polyodon spathula* historically ranged throughout the Mississippi River drainage into the Missouri River as far north as Montana (Gengerke 1986). Throughout their range, paddlefish supported commercial and recreational fisheries (Carlson and Bonislawsky 1981), but today the commercial and recreational harvest is far below historical levels (Gengerke 1986). The declining abundance and range of paddlefish are due largely to habitat alterations (Sparrowe 1986) and commercial fishing (Carlson and Bonislawsky 1981) and have caused some states to impose moratoriums (Reed et al. 1992), restrict harvest (Combs 1986), and initiate stocking programs to restore or establish paddlefish populations (Graham 1986). In 1989, the U.S. Fish and Wildlife Service was petitioned to list the paddlefish as threatened under the Endangered Species Act because of habitat loss and overexploitation (Allar-

dyce 1991). Although the petition was not granted, the listing effort emphasized the need to develop life history information and baseline data for the remaining populations, particularly in reservoirs.

The upstream migrations of spawning paddlefish were first documented by Purkett (1961, 1963) and subsequently noted throughout their range (Robinson 1966; Rehwinkel 1978; Pasch et al. 1980; Lein and DeVries 1998; Paukert and Fisher 2001b). Environmental cues associated with upstream spawning migration are thought to be a combination of water temperature, photoperiod, and rising water level or increasing discharge (Southall and Hubert 1984; Russell 1986; Paukert and Fisher 2001b). Most studies have focused primarily on riverine populations, with little attention to reservoir populations. However, reservoir paddlefish populations may exhibit seasonal migrations similar to those of riverine populations (Combs 1982; Paukert and Fisher 2000).

Our objective was to assess the site fidelity and seasonal movement patterns of naturally recruited adult paddlefish in South Dakota's Lake Francis

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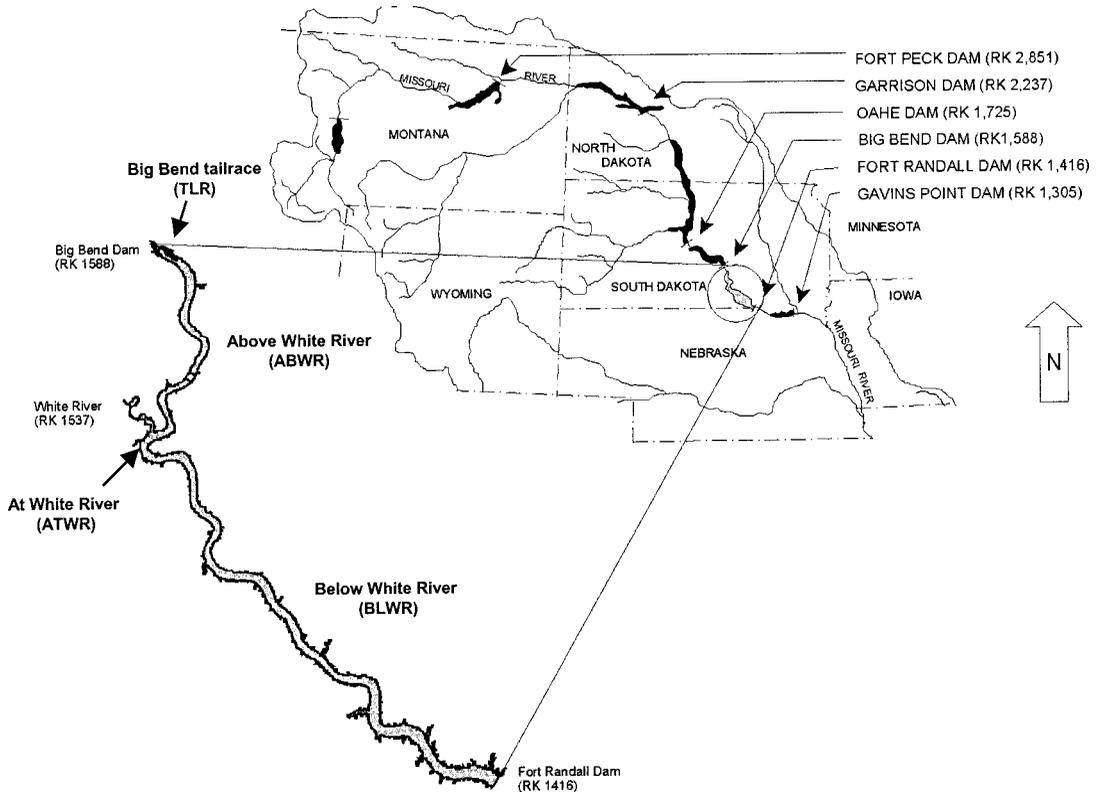


FIGURE 1.—Lake Francis Case, South Dakota, bounded by the Fort Randall Dam at its lower end and the Big Bend Dam at its upper end. The White River enters Lake Francis Case 51 river kilometers (RK) downstream from Big Bend Dam. Reservoir areas are as follows: Big Bend tailrace, above the White River, at the White River, and below the White River.

Case. This study would thus provide information that may prove essential to future paddlefish restoration efforts in the Missouri River's main-stem reservoirs. While our study was not designed to determine habitat use by paddlefish in Lake Francis Case, we were interested in knowing which particular reservoir areas were used seasonally. In particular, we wanted to determine whether paddlefish returned to the same areas during the spawning season, whether these fish concentrated in particular areas when they were not spawning, and whether they exhibited a primary direction of movement (i.e., upstream or downstream) during different seasons.

### Study Area

Lake Francis Case was formed by Fort Randall Dam and extends upstream as far as Big Bend Dam (Figure 1). Fort Randall Dam became fully operational in 1952 and reached an annual flood control level of 411 m above mean sea level in 1957. At base elevation, Lake Francis Case is 170 km long

and has a mean width of 1.86 km, a surface area of 320 km<sup>2</sup>, and a mean depth of 15 m. Bottom substrates include sand, silt, gravel, and shale. Most riverine-type habitats—such as backwaters, oxbows, and side channels—are absent from the reservoir, which is characterized by large annual water level fluctuations because it is drawn down each fall to provide storage capacity for spring flood waters and upstream hydropower production.

For about 7 years preceding the completion of Big Bend Dam in 1963, paddlefish in Lake Francis Case supported a recreational fishery; the population declined thereafter due to low recruitment (Unkenholz 1986), and harvest is now prohibited. Fingerling paddlefish were stocked beginning in the mid-1970s (Graham 1997) to restore their numbers to levels that would again support a recreational fishery. Graham (1986) discussed paddlefish stocking strategies in reservoirs without natural spawning areas and reported that maintenance stockings were an effective strategy for establishing spawning runs even when a suitable spawning

habitat was unavailable. A goal of Lake Francis Case paddlefish stocking was to establish a run of paddlefish into the White River, the only major tributary to the reservoir and an area where paddlefish historically concentrated (and may spawn) during the spring spawning season.

### Methods

We captured paddlefish in floating monofilament gill nets that measured 3.3 m  $\times$  100 m and had mesh sizes of 125 and 150 mm (bar measure) and that were continuously monitored. Captured fish were immediately removed from the net and held in a boat-mounted live well until they could be processed. Each fish was measured from the anterior portion of the eye to the fork of the tail (EFL; Ruelle and Hudson 1977) and tagged with a numbered monel jaw tag. The sex of each fish was determined from external characteristics, including the presence (male) or absence (female) of tubercles on the head and cheek and the production of milt or eggs, as well as by feeling for eggs through the oviduct. Fish of undetermined sex were excluded from our study.

Using the procedures described by Hart and Summerfelt (1975), we implanted each fish with a 50-month sonic transmitter (Sonotronics, Tucson, Arizona) having a detection range of 3,000 m. Each transmitter emitted a unique aural code that allowed for the identification of individual fish. On 13–14 May 1994, we implanted transmitters into 8 male paddlefish (range, 1,250–1,400 mm EFL) and 10 female paddlefish (range, 1,175–1,325 mm) that were collected in the White River and its confluence with the reservoir. Paddlefish presumably congregate near the White River in spring because the environmental cues (e.g., water temperature and flow) that lead to spawning are present. However, there is little evidence of spawning, most likely because of the limited spawning substrate (C. Stone, South Dakota Game, Fish, and Parks, personal communication). On 18–20 May 1994, we implanted transmitters in an additional five male paddlefish (range, 1,250–1,375 mm) and one female paddlefish (1,300 mm) collected in the Big Bend Dam tailrace. Paddlefish presumably congregate in this area during the spawning season because the Big Bend Dam blocks their migration to historical spawning locations. On 11–12 May 1995, to increase the sample size of fish implanted at the Big Bend Dam site, we implanted transmitters in five male paddlefish (range, 1,350–1,425 mm) and three female paddlefish (range, 1,150–1,275 mm). After surgery, each fish was held next

to the boat until it exhibited a strong swimming response, whereupon it was released.

We relocated transmitter-tagged fish (hereafter referred to as tagged fish) from May to November of 1994 and from March to November of 1995 and 1996. The reservoir was divided into four areas in which a crew could normally locate all of the paddlefish during an 8–10-h day. Each of the four zones was searched monthly by boat, with equal effort. The order of searching was based on logistical (e.g., weather and time) constraints. Beginning at one end of a reservoir zone, we stopped at 1-km intervals to listen for fish with a digital receiver (Sonotronics model USR-5W) and a directional hydrophone (Sonotronics model DH-2). Fish were considered located when signal strength could be heard equally well in all directions. From May 1994 to July 1995, the location of each fish was plotted on U.S. Army Corps of Engineers maps after visual triangulation of prominent terrestrial landmarks and features such as rivers, creeks, and bays. After July 1995, fish locations were recorded with a Global Positioning System receiver.

We defined four seasons with respect to paddlefish sampling: prespawning, spawning, postspawning, and winter. These seasons were characterized by both fish behavior and the environmental cues related to spawning. The prespawning season was defined as the period of increased long-distance movements upstream associated with increasing water temperature and photoperiod (1 March–30 April). The spawning season included the period when water temperatures were between 13°C and 18°C and fish were known to congregate in presumed spawning areas (1–31 May; however, we were unable to determine whether the tagged fish actually spawned during this season.). In the postspawning season, water temperature exceeded 18°C and fish exhibited downstream movements (1 June–30 September). The winter season began when the water temperature started to decline and lasted until our last tracking session of the calendar year (1 October–30 November).

Each paddlefish location was recorded as being in one of four reservoir areas: the Big Bend Dam tailrace (<4.8 river kilometers [rkm] downstream from Big Bend Dam), above the White River (from the Big Bend tailrace 48 rkm downstream to the White River confluence), the White River confluence (the 1.6-rkm area where the White River enters Lake Francis Case), or below the White River (from the White River confluence 115 rkm downstream to Fort Randall Dam; Figure 1). We also

recorded the direction of movement for each fish in reference to its location during the previous month's survey, that is, upstream, no change, or downstream.

**Data analysis.**—We quantified the use of reservoir areas by individual paddlefish by calculating the proportion of observations within each of the four reservoir areas ( $i$ ) for individual paddlefish each season ( $r_i$ ). We calculated this index for each fish in each season so that all fish would be equally weighted, thereby eliminating the possibility that one fish with many observations would unduly influence the index. In addition, we determined the proportion of the reservoir within area  $i$  ( $p_i$ ) by dividing its linear distance (in rkm) by the total linear distance of the reservoir. For example, the Big Bend tailwaters extends 4.83 linear rkm and Lake Francis Case is 167.44 rkm long; therefore, the  $p_i$  for the Big Bend tailwaters was 0.029. The area of the reservoir was defined in terms of linear rkm because the reservoir is of similar width (i.e., 1 km) in all reservoir areas. To determine whether males and females used reservoir areas similarly, we used a repeated-measures analysis of covariance (ANCOVA). In this analysis, the dependent variable was  $r_i$ ;  $p_i$  was used as the covariate because we would expect  $r_i$  to increase as  $p_i$  increased. Because we had many observations on our 32 individual fish, the repeated measure was the individual fish. Comparisons were made between implant sites (Big Bend Dam and the White River) for each season. When the mean proportion of observations ( $r_i$ ) is plotted against the proportion of the reservoir each habitat represents ( $p_i$ ), points above the 1:1 (45°) line (i.e., where  $r_i > p_i$ ) suggest that paddlefish used this area more than would be expected, whereas points below the 1:1 line ( $r_i < p_i$ ) suggest that these fish used this area less than would be expected.

To quantify the direction of movement, we determined the proportion of movements in a given direction (i.e., upstream, downstream, or no change) for each fish and season. By calculating a mean for each fish in each season, all fish were weighted equally, thus eliminating any undue influence of an individual fish with many observations. In the direction analysis, a repeated-measures analysis of variance (ANOVA) was used because multiple observations were recorded for each fish. All interaction terms were evaluated (type III sums of squares) prior to investigating the main effects. In all analyses, a mixed model was used (PROC MIXED in SAS; Littell et al. 1996) because this analysis does not require the assumption of homogeneity of variance.

TABLE 1.—Results of the repeated-measures analysis of covariance testing whether paddlefish use of the reservoir areas in Lake Francis Case, South Dakota, differed between sexes for each tagging site (Big Bend or White River) and season.

| Season and tagging site | F    | Degrees of freedom |             | P     |
|-------------------------|------|--------------------|-------------|-------|
|                         |      | Numerator          | Denominator |       |
| Prespawning             |      |                    |             |       |
| Big Bend                | 6.52 | 1                  | 48          | 0.014 |
| White River             | 6.81 | 1                  | 67          | 0.011 |
| Spawning                |      |                    |             |       |
| Big Bend                | 1.76 | 1                  | 51          | 0.190 |
| White River             | 2.74 | 1                  | 46          | 0.105 |
| Postspawning            |      |                    |             |       |
| Big Bend                | 2.08 | 1                  | 39          | 0.157 |
| White River             | 0.03 | 1                  | 64          | 0.868 |
| Winter                  |      |                    |             |       |
| Big Bend                | 0.00 | 1                  | 34          | 0.959 |
| White River             | 0.00 | 1                  | 48          | 0.947 |

We used logistic regression to determine whether the proportion of paddlefish returning to their original capture site differed between sexes, tagging sites, or year of return (i.e., the proportion returning 1 and 2 years after implantation). In this analysis, we used an events/trials format in SAS (PROC LOGISTIC; Stokes et al. 1997). In all analyses, we judged a result to be significant if  $P$  was less than or equal to 0.05.

## Results

Between May 1994 and November 1996, 32 ultrasonic-tagged paddlefish were relocated 731 times, with individual contacts ranging from 17 to 25 times. Male paddlefish tagged at the Big Bend tailrace site were relocated 206 times and females 76 times; males tagged at the White River site were relocated 199 times and females 250 times. No tagged paddlefish shed their tags or died throughout the 3-year study.

### Reservoir Habitat Use

Male and female paddlefish used reservoir habitat similarly across all seasons except in the pre-spawning period; use of reservoir areas differed by sex both for fish implanted at the Big Bend site and for those implanted at the White River site during this season (Table 1). However, paddlefish use of reservoir areas did not differ between sexes for any other season or tagging site (Table 1). Because male and female paddlefish used reservoir areas differently during the pre-spawning period, we separated fish by sex for this analysis. Pre-spawning male paddlefish tagged at the Big Bend site typically remained in the upper portion of Lake

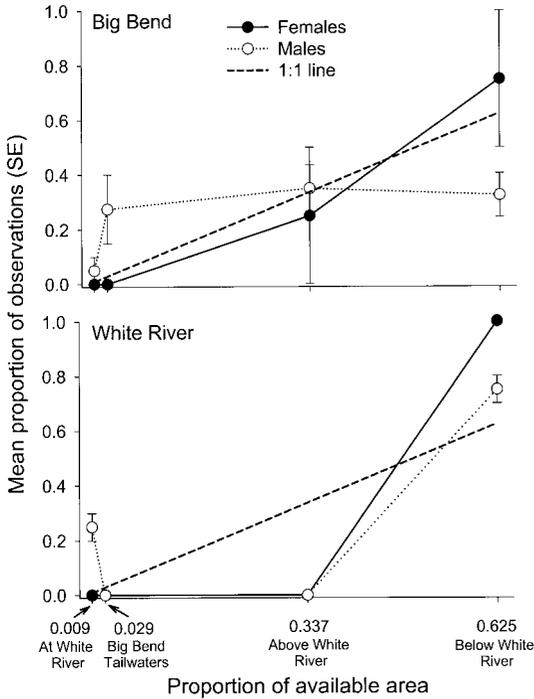


FIGURE 2.—Mean ( $\pm$ SE) proportion of locations of transmitter-tagged paddlefish in different reservoir areas of Lake Francis Case, South Dakota, during the pre-spawning season, by initial tagging site (the Big Bend tailwaters [upper panel] or the White River [lower panel]). Values on the x-axis are not evenly spaced because the reservoir areas were not equal in size. Mean values above the dashed line represent instances in which paddlefish used the reservoir area in a higher proportion than availability would indicate; values below the line represent instances in which paddlefish used the reservoir area in a lesser proportion.

Francis Case, primarily in the White River and the Big Bend tailwaters (Figure 2). No females implanted at the Big Bend site were located in the Big Bend tailwaters or the White River during the pre-spawning season (Figure 2). However, all 10 of the female paddlefish tagged at the White River site were located below the White River during the pre-spawning season, and 5 of the 7 males located during the pre-spawning season were at the White River (Figure 2).

The paddlefish located during the spawning season typically used the areas above and below the White River less than would be expected (Figure 3). Of the 8 male and 10 female paddlefish tagged at the White River site, 4 males and no females were located above the White River during the spawning season. Paddlefish tagged at the White River site used the White River extensively during

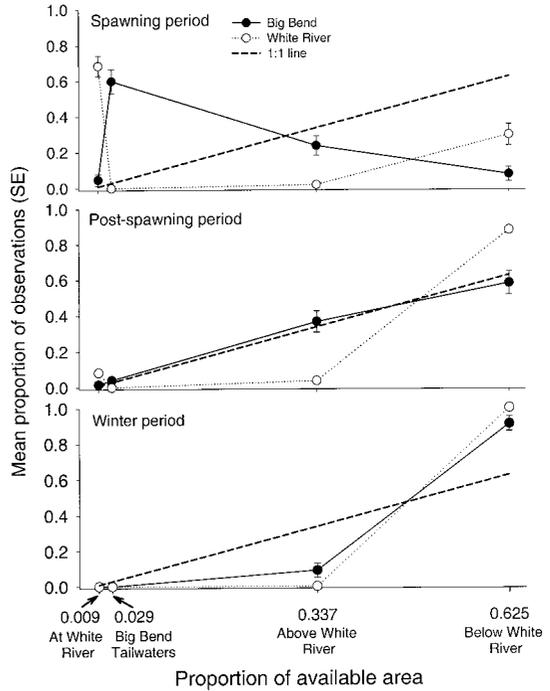


FIGURE 3.—Mean ( $\pm$ SE) proportion of locations of transmitter-tagged paddlefish in different reservoir areas of Lake Francis Case, South Dakota, during the spawning, postspawning, and winter seasons. Fish were initially tagged at the Big Bend tailwaters of the White River. Sexes are combined because there were no sex-related differences in reservoir area use. See the caption to Figure 2 for additional details.

the spawning season. Paddlefish tagged at the Big Bend site used the Big Bend tailwaters extensively (Figure 3). One Big Bend male and one female were relocated 1 and 2 years later, respectively, at the White River during the spawning season.

During the postspawning season, paddlefish typically retreated from the Big Bend tailwaters and the White River to other reservoir habitats. On average, 87.9% of the observations of paddlefish implanted at the White River site were recorded below the White River, whereas an average of 58% of the observations of the Big Bend fish were recorded in this area (Figure 3). During the post-spawning season, all male paddlefish implanted at the Big Bend site moved downstream at least 15 rkm below the tailwaters.

By winter, most paddlefish were found in the lower reservoir habitat below the White River (Figure 3). An average of 91% of the observations of paddlefish tagged at the Big Bend site were recorded below the White River, whereas all the observations of fish implanted at the White River

TABLE 2.—Results of a repeated-measures analysis of variance testing whether the mean direction of movement differed between sexes, implant sites (Big Bend or White River), or their interaction for paddlefish implanted with ultrasonic transmitters in Lake Francis Case, South Dakota. Separate analyses were done for each season.

| Variable                       | Prespawning |       |          | Spawning |       |          | Postspawning |        |          | Winter   |       |          |
|--------------------------------|-------------|-------|----------|----------|-------|----------|--------------|--------|----------|----------|-------|----------|
|                                | <i>F</i>    | df    | <i>P</i> | <i>F</i> | df    | <i>P</i> | <i>F</i>     | df     | <i>P</i> | <i>F</i> | df    | <i>P</i> |
| Direction                      | 3.56        | 2, 29 | 0.036    | 3.46     | 2, 45 | 0.040    | 59.64        | 2, 106 | 0.001    | 39.08    | 2, 42 | 0.001    |
| Implant site                   | 0.61        | 1, 12 | 0.451    | 0.23     | 1, 26 | 0.633    | 5.46         | 1, 24  | 0.028    | 0.01     | 1, 12 | 0.922    |
| Sex                            | 1.17        | 1, 28 | 0.289    | 0.75     | 1, 26 | 0.395    | 1.48         | 1, 25  | 0.236    | 0.03     | 1, 12 | 0.873    |
| Direction × implant site       | 0.77        | 2, 45 | 0.471    | 0.05     | 2, 47 | 0.949    | 1.81         | 2, 106 | 0.168    | 3.85     | 2, 42 | 0.029    |
| Direction × sex                | 3.64        | 2, 47 | 0.034    | 2.22     | 2, 45 | 0.120    | 1.07         | 2, 106 | 0.348    | 0.82     | 2, 42 | 0.449    |
| Implant site × sex             | 1.05        | 1, 16 | 0.321    | 0.09     | 1, 26 | 0.761    | 0.10         | 1, 25  | 0.752    | 0.08     | 1, 12 | 0.788    |
| Direction × implant site × sex | 0.00        | 1, 40 | 0.958    | 2.17     | 2, 45 | 0.126    | 0.40         | 2, 106 | 0.673    | 0.50     | 2, 42 | 0.610    |

site were recorded in this area (Figure 3). There were no observations of paddlefish in the Big Bend tailwaters or the White River during winter. By the last survey of each winter, at least 86% of all paddlefish locations were within 17.5 rkm of Fort Randall Dam.

#### Direction of Movement

The mean direction in which paddlefish moved varied by season and, in some cases, by sex and tagging location as well. During the prespawning season, the mean direction of paddlefish movement was not consistent between sexes (Table 2). Therefore, we separated the analysis for this season by sex. The mean proportion of upstream movement was higher in females than in males ( $F = 14.87$ ;  $df = 1, 39$ ;  $P = 0.0004$ ) and did not depend on tagging location ( $F = 0.86$ ;  $df = 1, 39$ ;  $P = 0.360$ ). The mean proportion of downstream movement was consistent between sexes and tagging sites ( $F = 0.38$ ;  $df = 1, 12$ ;  $P = 0.549$ ) and did not differ between sexes ( $F = 0.72$ ;  $df = 1, 12$ ;  $P = 0.412$ ) or tagging sites ( $F = 0.11$ ;  $df = 1, 12$ ;  $P = 0.752$ ). The mean proportion recorded as remaining in the same area did not differ among sexes ( $F = 0.25$ ;

$df = 1, 2$ ;  $P = 0.667$ ) or implant location ( $F = 1.00$ ;  $df = 1, 2$ ;  $P = 0.423$ ). However, only one female paddlefish location was recorded as evidencing no change in direction during the prespawning season. During the spawning season, the proportion of paddlefish movement downstream or upstream was less than that of fish remaining in the same area and did not differ between tagging locations or sex (Tables 2, 3). In contrast, during the postspawning ( $F = 59.64$ ;  $df = 2, 106$ ;  $P < 0.001$ ) and winter ( $F = 39.08$ ;  $df = 2, 42$ ;  $P < 0.001$ ) seasons, paddlefish exhibited strong downstream movements. During the postspawning season, paddlefish tagged at the White River site exhibited stronger directional responses than did fish tagged at the Big Bend site ( $F = 5.46$ ;  $df = 1, 24$ ;  $P = 0.028$ ; Table 2). Although the direction of movement was not consistent among tagging locations during the winter season (i.e., a two-way interaction; Table 2), paddlefish tagged at both sites exhibited the highest mean proportion of movement downstream during this period (Table 3). The mean proportion of movement did not differ between upstream and either upstream or downstream movement for paddlefish tagged at the

TABLE 3.—Mean (SE) proportions for direction of movement among seasons and between tagging sites and sexes for paddlefish in Lake Francis Case, South Dakota, 1994–1996. Means are based on the proportion of observations in which an individual fish moved in a given direction (i.e., upstream, downstream, or no change in position). Sexes were combined for all seasons except the prespawning period, when values differed between sexes (see Table 2). Values with no SE reflect the fact that there was only one observation. See text and Table 2 for statistical comparisons.

| Implant site | Direction  | Prespawning |             | Spawning    | Postspawning | Winter      |
|--------------|------------|-------------|-------------|-------------|--------------|-------------|
|              |            | Male        | Female      |             |              |             |
| Big Bend     | Upstream   | 0.41 (0.04) | 0.75 (0.14) | 0.36 (0.02) | 0.12 (0.01)  | 0.28 (0.03) |
|              | Downstream | 0.44 (0.06) | 0.42 (0.08) | 0.33 (0.00) | 0.39 (0.04)  | 0.62 (0.05) |
|              | No change  | 0.42 (0.08) | 0.50        | 0.47 (0.04) | 0.11 (0.01)  | 0.25 (0.00) |
| White River  | Upstream   | 0.48 (0.07) | 0.70 (0.07) | 0.40 (0.03) | 0.17 (0.02)  | 0.25 (0.03) |
|              | Downstream | 0.50 (0.25) | 0.38 (0.07) | 0.33 (0.00) | 0.53 (0.05)  | 0.72 (0.04) |
|              | No change  | 0.25        |             | 0.46 (0.05) | 0.11 (0.01)  | 0.17 (0.00) |

TABLE 4.—Proportion of paddlefish implanted with ultrasonic transmitters in Lake Francis Case, South Dakota, during the spawning season that returned to their original capture site during the spawning season 1 and 2 years after implantation. The last column is the proportion of fish returning to their original tagging site in each of the two subsequent spawning periods. The total number of paddlefish used in each calculation is in parentheses.

| Sex     | Implantation site   | Proportion of paddlefish returning |           |                    |
|---------|---------------------|------------------------------------|-----------|--------------------|
|         |                     | 1 year                             | 2 years   | Both 1 and 2 years |
| Males   | Big Bend tailwaters | 0.64 (11)                          | 0.33 (6)  | 0.17 (6)           |
|         | White River         | 0.57 (7)                           | 0.86 (7)  | 0.43 (7)           |
|         | Total               | 0.61 (18)                          | 0.62 (13) | 0.31 (13)          |
| Females | Big Bend tailwaters | 0.00 (5)                           | 0.00 (2)  | 0.00 (2)           |
|         | White River         | 0.44 (9)                           | 0.44 (9)  | 0.11 (9)           |
|         | Total               | 0.28 (14)                          | 0.36 (11) | 0.09 (11)          |

Big Bend site ( $F = 14.18$ ;  $df = 2, 24$ ;  $P < 0.0001$ ); however, paddlefish tagged at the White River site had the highest proportion of downstream movement and the lowest proportion of movements within the same area ( $F = 56.25$ ;  $df = 2, 32$ ;  $P < 0.0001$ ).

#### *Spawning Periodicity and Site Fidelity*

Paddlefish site fidelity during the spawning period differed between tagging site and sex but not years ( $\chi^2 = 16.39$ ;  $df = 4$ ;  $P = 0.019$ ). A greater proportion of males than females returned to the site where they were initially tagged ( $\chi^2 = 7.55$ ;  $df = 1$ ;  $P = 0.006$ ; Table 4). Paddlefish tagged at the White River site were about four times more likely (based on logistic regression odds ratios) to return at least 1 of the 2 years after tagging than paddlefish tagged at the Big Bend site ( $\chi^2 = 4.17$ ;  $df = 1$ ;  $P = 0.041$ ). However, the proportion of fish returning to their original capture locations did not differ between years (i.e., 1 or 2 years after implantation;  $\chi^2 = 4.71$ ;  $df = 2$ ;  $P = 0.095$ ). Only 1 of 11 females (9%) that were located in each of the 2 years after tagging returned to its original capture site in each of the 2 subsequent years, whereas 31% (4 of 13) of the male paddlefish returned in each of the 2 years after tagging (Table 4).

#### **Discussion**

Our study provided evidence that Lake Francis Case paddlefish exhibited distinct seasonal migrations and utilized different reservoir areas seasonally; except for the prespawning season, this behavior was generally similar between sexes. Paddlefish locations during the prespawning season indicated that males return to their initial tagging site before females. However, paddlefish utilized their initial capture locations during the spawning

season regardless of sex. Concentrations of paddlefish below barriers (e.g., dams) (Southall and Hubert 1984) or in potential spawning locations (Lein and DeVries 1998) during the prespawning and spawning seasons have been documented; however, little information exists on the sexual differences in movement and habitat use during this time. Our results suggest that males migrate upstream prior to females during the prespawning season, but both sexes generally utilized the Big Bend tailwaters and the White River during the spawning season. During the postspawning season, paddlefish typically exhibited strong downstream migrations from the Big Bend tailwaters and the White River to other reservoir areas. Females are believed to migrate downstream immediately after spawning whereas males may remain in the spawning areas longer (Russell 1986). In our study, the direction of movement was not influenced by sex, and both males and females appeared to migrate downstream to the area below the White River. Similarly, Paukert and Fisher (2001b) found that both male and female paddlefish in an Oklahoma reservoir system migrated downstream after the spawning season. During the winter season, all paddlefish exhibited downstream migrations to areas below the White River. Paddlefish typically concentrate in the deepwater areas in times other than spawning (Pitman and Parks 1994; Zigler et al. 1999; Paukert and Fisher 2001a). The reason why paddlefish would select the area below the White River over other reservoir areas (e.g., above the White River) is unclear. One possible reason is the typically low abundance of their food source (zooplankton) in the upper reservoir reaches (Marzolf 1990), as fishes may select reservoir areas based on resources or favorable environmental conditions (Wilkerson and Fisher 1997). We do not believe that environmental con-

ditions (e.g., water flow or habitat) played a large role in paddlefish distributions in Lake Francis Case because there is little flow in the reservoir during this period and there appeared to be no distinct differences in habitat between these two areas.

Male paddlefish in Lake Francis Case exhibited greater fidelity to their original tagging sites than did females. Males may have the potential to spawn annually, whereas females may not (Russell 1986), and a high proportion of males returned to their original tagging location during at least one of the two spawning seasons following tagging. In addition, 31% of males were located each of the following 2 years at their tagging location during the spawning season, compared with only 9% (1 fish) of females. While Lein and DeVries (1998) suggested that both riverine males and females may make annual spawning migrations, a telemetry study conducted in an Oklahoma reservoir revealed that all females moved upriver during spring and many mature males did not (Paukert and Fisher 2001b). Lake Francis Case paddlefish exhibited site fidelity during the spawning season, particularly for the White River; these results are similar to those of Lein and DeVries (1998) and Brantly (1987), who also noted site fidelity of spawning paddlefish in Alabama rivers. However, even in populations that exhibit strong homing behaviors, a third of the population may stray (Gerking 1959), which likely occurred in our study.

Paddlefish still exhibited fidelity to original capture locations during the spawning season, despite the fact that environmental cues for spawning were not evident every year. Although the White River exhibited limited flows in 1995 and peak flows in 1996, paddlefish previously tagged there staged at the mouth or moved a short distance up the river in both years. Similarly, 12 of the 14 paddlefish implanted at the Big Bend site bypassed the White River and moved into the Big Bend tailwaters during the spawning season in both years. Although water flows may dictate spawning migrations (Russell 1986) and may even override site fidelity (Paukert and Fisher 2001b), paddlefish in Lake Francis Case apparently have strong tendencies toward site fidelity.

Although paddlefish may migrate up to the Big Bend tailwaters and the White River, they may not spawn in those areas. We were unable to identify spawning habitat in or around the Big Bend tailwaters and suspect that these fish were actually attempting to access spawning areas upstream of Big Bend Dam. We did not document spawning in

the White River, presumably because there is limited spawning substrate in this area (Stone, personal communication). Unkenholz (1986) noted that paddlefish concentrated in the Oahe tailrace (i.e., the next upstream dam), but these runs diminished after Big Bend Dam was completed. Some of the fish that were harvested in the Big Bend tailwaters were likely once part of the paddlefish migration concentrated in the Oahe tailrace.

During the spring of 1997 (after the study ended), we located four of our tagged fish in Lewis and Clark Lake, the reservoir downstream of Lake Francis Case; this occurred after the emergency floodgates on Fort Randall Dam were opened because of high water flows. Such an occurrence suggests that paddlefish historically migrated farther downstream after the spawning season but that dams have reduced these downstream movements. Similarly, others have reported substantial migrations over dams (Russell 1986; Paukert and Fisher 2001a). A paddlefish from our study was caught in June 2001 below Barkley Dam on the Cumberland River, Kentucky; this fish traveled an estimated 1,900 rkm and passed five dams prior to capture. These observations may indicate extensive paddlefish movements in free-flowing rivers and that impediments to these movements (e.g., dams) now restrict the opportunities available to this species to reach spawning areas or other, more favorable habitats.

Our results suggest that adult paddlefish migrate and exhibit site fidelity to areas where environmental cues may trigger spawning attempts. Although rare, female paddlefish with free-flowing eggs have been collected in the White River during the spawning period (Stone, personal communication). Those stocking paddlefish to create a self-sustaining population may need to consider the possibility that the absence of suitable habitat (i.e., substrate) will limit reproduction even when there is site fidelity. Dams that block spawning migrations and isolate highly migratory populations reduce overall species fitness (Unkenholz 1986) and lower the likelihood of area recolonization if a catastrophic event were to occur. Our study suggests that paddlefish exhibit site fidelity to an area that may support reproduction, given adequate substrate. Restoration efforts (e.g., stocking and habitat manipulation) may need to focus on areas where paddlefish may spawn so that these fish can imprint to those areas in the future.

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